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nests that extends over hundreds of square kilometers.

What about humans and our closest evolutionary relatives? The most fluid societies of any nonhuman primate are found among chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), humanity's nearest living relatives. Chimpanzee communities, for instance, are rarely seen together as a whole. Instead, subgroups of various sizes constantly coalesce and split based on moment-to-moment foraging and socializing needs. Subgroups of adult male chimpanzees separate from the group to cooperatively hunt mammalian prey or to patrol their border, and male-female dyads split off from the group to engage in sexual consortships with minimal mating competition. As a consequence of such fission–fusion processes, the composition of traveling chimpanzee parties is highly variable, often changing by the hour.

When it comes to our own species, there is no doubt that, by nature, we form fission–fusion societies. And nor is this merely a reflection of our current, highly mobile lifestyle within industrialized settings. More than 99% of human history was spent in a hunter-gatherer existence, characterized by dynamically shifting social groupings at multiple levels. At the highest tier in hunter-gatherer societies is the ethno-linguistic group or 'tribe', formed by several local 'bands' that fuse together when resources like water are clustered during dry seasons. Bands themselves, which are made up of around 30 individuals, break up into smaller foraging parties during daily forays out from a base camp. While some individuals remain at the camp to watch over youngsters and tend the old or injured, the foraging parties gather edible plant material and hunt animals, afterward bringing the bounty back to a central place for sharing and redistribution.

Hunter-gatherer societies exhibit division of labor, though mostly between the sexes and not to the extent of the highly specialized castes of social insects. Hunting, for instance, is typically — but not universally — done by men, while gathering is done by women and in part by men too. Pair bonds, non-existent in the promiscuous chimpanzees and bonobos, enable men and women to assume distinct but complementary ecological roles, splitting apart during the day and then pooling their assorted resources when they convene at night. Aside from such ecological reasons for fission–fusion among hunter-gathers, social reasons also abound. One of the most common is verbal disputes and fighting, which can result in individuals switching camps. The Hadza of Tanzania insist that fissioning into smaller camps is a surefire route to 'less bickering'.

What does gossip have to do with fission–fusion? Gossip, in the strict sense of talking about third parties who are elsewhere at the time of the dialogue, appears to be uniquely human. Of even greater interest, most of our species' conversations — over two-thirds by some study estimates — focus on gossip. But why is gossip necessary? Far from being mere small talk, gossip serves myriad vital functions within our fission–fusion societies, both at the individual level and at the group level. Gossip can facilitate social cohesion in the face of repeated separations, reminding individuals of the bonds they have with distant others. And it can also allow information to percolate through the group about the trustworthiness of each member, enabling listeners to keep track of others despite limited first-hand observation. Gossip, therefore, and maybe even language more generally, may have evolved specifically as an adaptation to the highly fission–fusion-oriented societies of our hunter-gatherer ancestors.

Where can I find out more?

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Primer

Evolution of sound localisation in land vertebrates

Christine Köppl

Pinpointing where a sound comes from may appear trivial to you. After all, we do it constantly without even thinking about it. Yet, by the time you become aware of that bird call from the tree outside the window or the footsteps of your child running down the stairs, your brain has been hard at work deducing the directions these sounds came from by using a number of different cues. Unlike vision, the sense of hearing cannot rely on a spatial image of the external world being projected onto the primary receptor surface and relayed to the brain. The inner ear works much like a spectrum analyser, with individual receptors being exquisitely sensitive to a narrow part of the audible frequency range, but conveying no information about the spatial origin of that sound. Thus, the onus is on the brain: it needs to determine where sound came from using indirect cues. How do humans and other animals do that? Until recently, it was thought that we understood at least one particular aspect of sound localisation — the neural processing of interaural (between the ears) time differences — fairly well. But conflicting results from work on birds and mammals has sparked a lively debate about whether there is only one or perhaps two fundamentally different mechanisms. I will use this specific example to illustrate how a broader look at the evolution of sound localisation and hearing in general can be instructive in identifying the constraints on specialised neural circuits and in deducing their evolutionary histories.

Let's get physical: the basics of sound localisation cues

Sound localisation has a lot to do with the relative dimensions of the listener and the sound waves to be localised, so some basic facts about the physics of sound propagation and diffraction need to be appreciated. The physical cues that are widely known to be

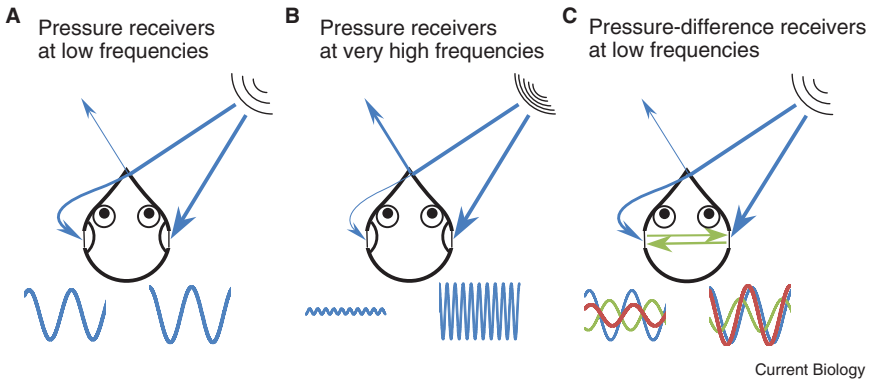

Figure 1. The binaural physical cues for sound localisation.

(A,B) The two panels illustrate the classic case of a listener with two pressure receiver ears — where sound reaches the eardrum only from the outside — which measure sound independently. In the example shown, a sound source emits from the right of the listener; the waveforms show the relative amplitudes and timing of sound reaching the left and right ear. (A) At low frequencies (below about 10 kHz for most animals), sound shadowing or diffraction by the head is negligible, resulting in very little amplitude difference at the two ears. The timing difference depends on the distance between the ears, but is always very small (below 1 millisecond). (B) At much higher frequencies with shorter wavelengths, diffraction by the head is significant, resulting in a large level difference between the ears. (C) If the middle ears are connected, they act as pressure-difference receivers. The receiver in this case is the eardrum. The crucial feature is that the eardrum is exposed to multiple sound paths reaching it not only from the outside, but also from the inside. The most common case is an additional sound path entering through the contralateral eardrum and passing through the head (green arrows) — literally in one ear and out the other! The net eardrum vibration (red waveforms) is the sum of the sound pressure impinging on the outside (blue curves) and the inside (green curves) of the eardrum. Depending on the lengths of the different sound paths and the attenuation across the head, sound waves will add constructively or destructively and the resulting eardrum vibration may vary significantly with incoming sound direction (only one direction is illustrated here). Furthermore, both interaural time and level differences are enhanced compared with those derived from straightforward pressure receivers (compare A and C).

used in sound localisation fall into two categories: timing cues and diffraction cues.

Interaural time differences arise from different sound path lengths to the two ears. Moving a sound source further off to one side of the listener induces a progressively larger interaural time difference. Binaural comparison of the timing of the two ears' independent inputs can thus provide an indirect cue to sound origin along the horizontal plane or azimuth. This appears very straightforward until one considers the actual head sizes of animals, which determine the extent of the time difference. The small heads of mice, lizards, songbirds and the like generate interaural time differences of the order of one hundred microseconds — one ten-thousandth of a second! Even for comparatively large-headed animals such as horses, humans or alligators, interaural time differences remain smaller than one millisecond. This pushes the limit of what neurons can resolve, so having a small head is a disadvantage.

Diffraction cues are sound level cues, generated from diffraction or sound shadowing by structures in the sound path. Interaural level differences arise due to diffraction by the head and body, resulting in different levels of sound reaching the two ears (Figure 1B). The extent of the difference depends both on head size and sound frequency. As a rule of thumb, for a mouse-sized animal, frequencies above 10 kHz need to be present and audible to make use of interaural level differences. Diffraction cues can also be generated monaurally by external ear structures such as earlobes or pinnae. Their dimensions and intricate shape determine which frequencies are most effectively deflected and how much this effect varies with incoming sound direction.

Size is undoubtedly an important determinant of the cues available for sound localisation. Much of the classic literature on the subject made the case that with a small head and a hearing range restricted to below about 10 kHz, there are no directional cues to speak of (Figure 1A). But that is actually not true, as insects, birds, frogs and lizards have taught us. These animals have ears which work according to the physical principle of pressure-difference receivers (Figure 1C). Acoustic interaction between the two ears is the most common way to establish a pressure-difference receiver, but the resulting neural input to the brain from one such receiver can provide significant (monaural) directional information. Binaural comparisons provide additional cues. In fact, for the same head size, two reciprocally acting pressure-difference receivers can significantly boost both interaural time and level differences, compared with those derived from straightforward pressure receivers (compare Figures 1A and 1C). Perhaps best of all, pressure-difference receiving does not require very high frequencies and is most effective in small animals. This is because sound transmission suffers less attenuation the shorter the distance is across the head and the lower the frequency.

Now imagine that all of the cues outlined above could in principle be used simultaneously for localising sound and you will appreciate that the brain has its work cut out! But not every cue is as good as any other. One would predict that small animals should rely more heavily on directionality provided by a pressure-difference receiver mechanism, unless they are able to hear frequencies high enough to provide significant monaural or binaural diffraction cues. Larger animals on the other hand enjoy inherently larger interaural time differences and do not need to hear frequencies as high to make use of both monaural and binaural diffraction cues. All of this becomes very relevant when we try to understand how the sensitivity for sound direction has evolved in vertebrates and how the way the human brain localises sound has been shaped by its evolutionary history.

The many tales of how to hear airborne sound

In the past 30 years or so, profound insights into the mechanisms of hearing in vertebrates have come from an unexpected direction. New fossil finds and cladistic analyses have prompted a re-interpretation of

the evolution of the middle ear bones, eardrum and spaces around the inner ear. These structures are all vital in forming the tympanic middle ear, an impedance-matching apparatus for the transmission of airborne sound to the fluid-filled inner ear. It is now believed that the tympanic middle ear evolved several times independently, after the major vertebrate lines had already separated. Does this mean that early land-living vertebrates did not hear? Yes and no. Animals without a tympanic middle ear would have been nearly deaf to airborne sound, so they had no hearing in the sense that we commonly understand it today. However, they most likely already had a dedicated receptor, the basilar papilla or cochlea, and 'listened' to groundborne vibration and loud airborne sound below about 1 kHz. In other words, basic low-frequency hearing came first, sensitive and high-frequency hearing followed later.

Surprising as the conclusion about a relatively late arrival of the tympanic middle ear initially was, it suddenly made sense of a previously unexplained variation in inner-ear structure. Present-day amphibians, turtles, lepidosauromorphs (lizards and snakes), archosauromorphs (birds and crocodilians) and mammals all have distinct cochlear specialisations. These divisions fit the proposed independent lines of middle-ear evolution, suggesting that once a nascent sensitivity to airborne sound existed, coevolution between middle and inner ear was triggered, leading to improved sensitivity and an increase of the hearing range towards higher frequencies, independently in each of the major vertebrate clades.

We are just starting to appreciate the implications of this for the central auditory system. After decades of implicitly assuming and searching for common neural mechanisms in auditory processing, the possibility of independently derived, different mechanisms now needs to be considered for central auditory processing, too. We should carefully look at the evidence, however. Even assuming that much of the sophisticated auditory processing in the brains of modern vertebrates is the result of independent evolution does not necessarily mean the mechanisms at work are different. If the selective pressures were similar, the outcomes may be convergently similar as well. The current debate about how interaural time differences are processed neurally is an instructive example of this conundrum.

The neural basis of interaural time difference processing

Historically, much of the research on interaural time difference processing has focused on the barn owl, an avian nocturnal predator that is renowned for its exquisite hearing and that relies on sound localisation for prey capture. The neural processing of interaural time differences in the owl conforms to the principle of coincidence detection between input delay lines which had been suggested as early as the 1940s by L.A. Jeffress on theoretical grounds (Figure 2A). In the owl, a large array of coincidence detector cells together forms a map of interaural time differences. This is relayed to higher brain centres where it provides the horizontal coordinates for a topographic neural representation of the auditory space around the animal.

Neural processing of interaural time differences in the barn owl is compelling in the simplicity of the underlying principles, but it is also one of the most specialised neural circuits known. Every element, beginning with the sensory cells in the inner ear, shows extreme adaptations towards achieving a most incredible temporal resolution: an individual coincidence detector cell in the owl's brainstem responds to only a small part, typically about 100 microseconds, of the owl's total range of interaural time differences. No other animals' neurons are known to achieve such selectivity, although similarly organised circuits exist in the brainstem of other birds and of mammals. Upon closer examination, however, these circuits may be less similar than originally thought. Recent work on small mammals, such as gerbils and guinea pigs, has suggested salient differences to the owl and these findings have sparked a lively debate about whether there is a common mechanism of interaural time difference processing or not. Most importantly, precisely timed inhibitory inputs, in addition to the excitation from each ear, are thought to be crucial in small mammals and neural delay lines have not been clearly shown to exist. This has led to an alternative hypothesis in which interaural time differences are not represented as a fine-grained map in each brainstem hemisphere but are instead coded in the relative overall excitation of the two brainstem hemispheres (Figure 2B). Many open questions remain, not least concerning how this alternative code may be read out by higher brain centres and used towards the creation of a representation of auditory space. But a code based on overall hemispheric excitation appears to solve the classical dilemma of small animals that have a very small range of interaural time differences and face the formidable task in creating individual neural responses that are suitably selective to resolve the small timing differences involved.

An obvious problem with this interpretation is that small birds such as the chicken (which has a similar head size to the gerbil) show all the hallmarks of a Jeffress-type neural circuit for coding interaural time differences, very similar to the barn owl. Indeed, data from several bird species and the closely related alligator are remarkably consistent. If small birds can use this mechanism for sound localisation, why can't small mammals? One explanation may be different evolutionary histories of sound localisation. Did those brainstem circuits for interaural time difference processing perhaps evolve independently in birds and mammals? Much of the classic literature assumes that the relevant brainstem nucleus is homologous between birds and mammals. But this assumption is based entirely on functional similarity, the basis for analogy but not homology. In fact, the structure is located differently in the mature brains and was named differently — nucleus laminaris in birds and medial superior olive in mammals — indicating that early anatomists ignorant of its function didn't see any immediate relationship. Developmental studies on the embryonic origin of both nuclei might in future help to resolve the question whether they are homologous or convergent.

Another approach to elucidate the origins of neural circuits processing interaural time differences is to examine the remaining major groups of land vertebrates, amphibians, turtles and lepidosauromorphs (lizards and snakes). How do they

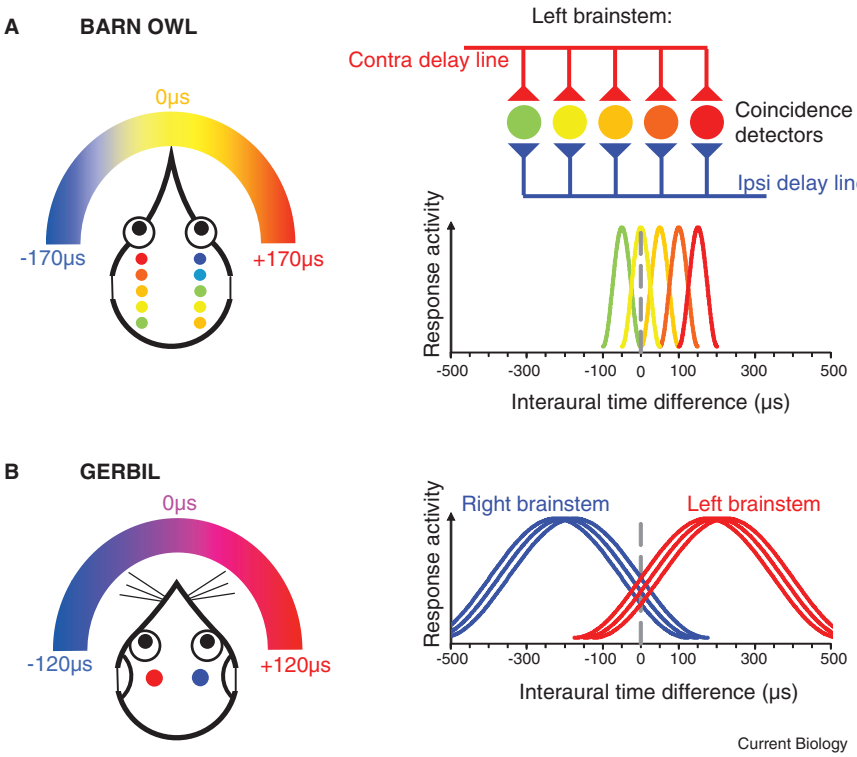

Figure 2. Two suggested mechanisms for the coding of interaural time differences at the brainstem level.

(A) In the barn owl, each half of the brainstem contains a map of interaural time differences, corresponding to sound sources mostly in the contralateral acoustic hemifield. This map is created by the basic circuit illustrated for the left brainstem. Auditory-nerve input is relayed from both ears to cells (coloured circles) which act as coincidence detectors, themselves firing maximally when action potentials from both ears arrive simultaneously. The inputs arrive along nerve-cell axons (blue and red) which vary systematically in their length on their way to the different target cells. Because longer axons take more time to transmit their signals, they act like delay lines and introduce cellular time delays. These delays, when compensated for by matching acoustic delays from acentrally located sound sources, lead to maximal firing at that particular interaural time difference. Typical responses of barn owl coincidence detector neurones are shown below the circuit diagram, as a function of interaural time difference. Together they cover the interaural time difference range experienced by the owl and form a topographic representation of the auditory azimuth. (B) In the gerbil, the responses of neurones in one half of the brainstem are all similar and show only broad selectivity compared to the interaural time difference range experienced by the animal. It is thought that higher-order brain areas compare the relative activity levels of both brainstem sides to derive a correlate of sound source location.

localise sound and, specifically, process interaural time differences? Are the principles shared or not? Unfortunately, very few studies have addressed binaural auditory processing in these species. At present it is not even clear whether an auditory brainstem nucleus that processes interaural time differences is consistently present, let alone what its circuitry and physiology may be.

Neural tissue does not fossilise, so the condition of ancestral neural circuits can only be guessed at. However, skull and middle-ear bones can provide important indirect pieces in the puzzle of what different vertebrate animals may have heard and how they may have localised sound. Let's look at open questions and arguments relevant to the discussion about mechanisms of sound localisation in general and the processing of interaural time differences in particular.

In one ear and out the other: how common?

The pressure-difference receiver mechanism is a way for small animals to increase their interaural differences. Thus, it represents an alternative, non-neural solution to the classical dilemma outlined above for small mammals. The idea is far from new, but has largely been ignored because extant mammals do not use it. Consequently, experimental evidence relevant to its possible use in vertebrates is limited and the extent of any enhancement is still controversial. The problem is that the efficiency of sound transmission across the head is crucial and impossible to predict from theory. Recent data from lizards have surprised even the experts in showing just how efficient this coupling can be. In some of these animals, sound literally goes in one ear and, almost unattenuated, out the other! While previous data from birds had been inconsistent and fraught with experimental artefacts, the new lizard measurements provide a clear proof-of-principle for the pressure-difference receiver mechanism in vertebrates. The big remaining question is: how common is it and how efficient is it? For extant species, this can be and needs to be addressed experimentally. For fossil forms, we now need to at least consider the possibility. Even a moderate enhancement of interaural cues would presumably provide a selective advantage for localising sound in small animals with a restricted high-frequency hearing range, for which diffraction cues are negligible.

I suggest that most of the early land vertebrates with nascent sensitivity for airborne sound are likely to have relied on the pressure-difference receiver mechanism. Interaural time differences should then have been a realistic cue for sound localisation even for small animals. Whether they are likely to have had a dedicated neural processing circuit is harder to say. We currently know very little about the concurrent processing of intensity and timing cues provided by two ears acting as reciprocal pressure-difference receivers. Relevant data are likely to come from studies on extant frogs and lizards.

Inferring function from fossils: when did mammals begin to hear really high frequencies?

Mammals are clearly in a class of their own when it comes to hearing range, as they are able to hear much higher frequencies than other vertebrates. Not every single species does — and we humans are one of the exceptions — but most mammals hear well into the ultrasonic range, above 20 kHz. As a rule of thumb, 10 kHz is the upper limit for

non-mammals. The reason for this unique ability of mammals ultimately goes back to the middle ear; any inner-ear specialisations would have followed later. The mammalian three-ossicle middle ear, by virtue of its construction, is able to transmit much higher frequencies to the inner ear than the single-ossicle types that other land vertebrates have. Furthermore, extant mammals, even very small ones, do not have pressure-difference receivers. Sound paths through the head do not exist, as each middle ear forms an enclosed cavity (the bulla) connected to the mouth cavity only via the narrow Eustachian tube which is usually closed. For sound localisation, extant mammals appear to rely on high-frequency diffraction cues; only if the animal is large enough and also hears low frequencies, may it use interaural time differences in addition. But is this also the ancestral condition for mammals? There are good arguments against that; both the hearing of really high frequencies above 10 kHz and the isolation of the middle ears from each other may be fairly recent events that occurred late in mammalian evolution.

Two of the three mammalian middle-ear ossicles very gradually transformed from jaw-joint bones over a period of tens of millions of years — incidentally one of the best documented fossil histories. Functionally, it is largely a matter of conjecture what these animals may have heard — there is simply no modern equivalent for the transitional forms. It is mostly agreed that some sensitivity for airborne sound, perhaps into the kilohertz range, was present. A more difficult question and one salient for sound localisation is: when did mammals begin to hear much higher frequencies than other vertebrates? This would have been the point where diffraction cues became a serious option. Opinions are deeply divided on this. Based on endocasts of fossil cochleae, some have argued for a late acquisition of sensitivity to frequencies beyond 10 kHz in therian mammals (marsupials and placentals) only. Others have postulated a much earlier and rather sudden onset, something akin to a transposition of the hearing range to high frequencies, at the expense of any sensitivity much below 10 kHz.

An argument advanced in favour of such early high-frequency hearing is that early mammals (mammaliaformes) were small mouse-sized animals for which very high-frequency hearing would have meant a powerful selective advantage in enabling them to localise sound. But this ignores the possibility that they were able to localise quite well using a pressure-difference receiver mechanism. A bulla enclosing the middle ear is typical for therian mammals only, and is likely to have evolved late and several times independently. If early mammals indeed made use of a pressure-difference receiver mechanism for sound localisation, anything leading to a sudden loss of the working lower-frequency system would have been a disadvantage.

A likely scenario was that early mammals relied on similar sound localisation mechanisms as extant lizards or birds — that interaural time differences played a potentially important role. Only when the coupling between the middle ears was reduced, possibly triggered by an increase in brain size, did the selective pressure increase for those animals in transition to de-couple the middle-ear ossicles from their jaw-joint association, if this improved the efficiency of high-frequency transmission. There is evidence that this may even have happened several times independently, including in some extinct mammalian branches.

Summary

The story of the evolution of hearing in land vertebrates is fascinating but complex. The water-to-land transition changed the physical environment in which hearing happens so dramatically that both the peripheral receptor structures and the central auditory circuits underwent a revolution, leading to the sensitive hearing of higher-frequency airborne sound. This (r)evolution took a very long time indeed. Most of it happened after the early divergence of the major clades of land vertebrates. Hearing, at least hearing as we commonly understand it today, is the youngest of the major senses and much of its evolutionary history is not shared between amphibians, lepidosauromorphs (lizards and snakes), archosauromorphs (birds and crocodilians) and mammals. There was no linear evolution of complexity from 'lower' to 'higher' vertebrates. We are only just beginning to appreciate the implications of this for central auditory processing. There is no consensus, yet, on the evolution of sound localisation. The multitude of physical cues involved in sound localisation means that different selective pressures interact and need to be considered. The use and neural processing of interaural time differences is just one example. It has taught us that long-standing assumptions, such as the homology of the mammalian medial superior olive and the avian nucleus laminaris, need to be questioned and that important insights may arise from unexpected directions, such as the paleontology of middle-ear ossicles. There is still much to discover.

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